Courtship Among Sterile and Wild *Ceratitis capitata* (Diptera: Tephritidae) in Field Cages in Hawaii and Guatemala

D. R. LANCE,[1] D. O. MCINNIS,[2] P. RENDON,[3] AND C. G. JACKSON[4]

Hawaii Plant Protection Center, USDA-APHIS-PPQ, P.O. Box 1040, Waimanalo, HI 96795

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ABSTRACT Male–female interactions among three wild and three laboratory strains of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), were observed on caged trees in Hawaii and Guatemala. Sterile and wild males appeared comparable at attracting wild and sterile females into their territories and initiating courtship. Wild females, though, consistently accepted courtship overtures of wild males more readily (copulation occurred in 28% of 199 interactions) than they accepted those of sterile males (8% of 261 interactions). Depending on the strains involved, wild females were more likely to reject sterile (versus wild) males during the male's courtship display, after the male mounted the female, or both. Sterile females accepted sterile males in 23.8% of 407 interactions and wild males in 26.1% of 257. Periodicity of mating behavior varied somewhat among strains, but sterile flies did not mate consistently earlier or later in the day than did wild flies. Less-than-desirable levels of mating compatibility between sterile and wild *C. capitata* appear to result primarily from the relatively low rates at which wild females accept courtship overtures of sterile males.

KEY WORDS *Ceratitis capitata*, sterile insect technique, copulation, mating competitiveness

THE STERILE INSECT TECHNIQUE (SIT) is used increasingly in the United States and elsewhere for suppressing and eradicating populations of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann). SIT programs are successful to the extent that mass-produced, sterile males mate with wild females in target populations. Effects of laboratory colonization, artificial rearing environments, sterilization procedures (e.g., irradiation), and shipping and handling can cause mating behaviors of sterile males to differ somewhat from those of wild males (Bush et al. 1976, Ohinata et al. 1977, Ozaki and Kobayashi 1981, Lance et al. 1988, McInnis et al. 1996, Yuval 1998). Such differences can potentially reduce the ability of sterile males to compete with wild males for mates (Calkins and Ashley 1989).

In tephritids, such as *C. capitata*, mating compatibility of sterile males with wild females is problematic, because male courtship behavior is complex, and females actively choose their mates (Prokopy and Hendrichs 1979; Arita and Kaneshiro 1985; Whittier et al. 1992, 1994). Briefly, males initially locate a suitable microhabitat for calling (releasing pheromone), which is typically on the underside of a well-lit leaf (Prokopy and Hendrichs 1979). They produce and release a very complex pheromone (Jang et al. 1989) that attracts virgin females. Males often call in small aggregations that some authors have compared with the lek behavior of vertebrates (Prokopy and Hendrichs 1979, Whittier et al. 1992, Shelly et al. 1994, but see Saul and McCombs 1995). When a female approaches, the male initiates a courtship ritual that consists of head rocking and pulsed wing fanning (Feron 1962, Arita and Kaneshiro 1985, 1989, Briceño et al. 1996, Liimatainen et al. 1997). If the female is receptive, the male mounts her, and copulation ensues. Most females, though, solicit courtships from a number of males before accepting one as a mate (Prokopy and Hendrichs 1979, Whittier et al. 1992). Females may leave the courtship arena at any time. Even after being mounted, females often drop from the substrate and shake the male off before intromission occurs. Given this mating system, relatively minor discrepancies in the mating behavior of sterile males could substantially reduce competitiveness.

Results of recent research indicate that wild female *C. capitata* often mate more readily with wild males than with sterile, laboratory-reared males (Shelly et al. 1994, McInnis et al. 1996, Liimatainen et al. 1997, Cayol et al. 1999, but see Wong et al. 1983). Indeed, in field trials in which induced sterility has been monitored, sterile *C. capitata* have typically been no >10% competitive overall (Wong et al. 1992, McInnis et al. 1994; D.O.M. and P.R., unpublished data). In 1993, we ini-

[1] To whom correspondence should be addressed: Otis Plant Protection Center, USDA-APHIS-PPQ, Building 1398, Otis ANG Base, MA 02542.

[2] Tropical Fruit and Vegetable Research Laboratory, USDA-ARS, 2727 Woodlawn Drive, Honolulu, HI 96822.

[3] Guatemala Plant Protection Station, USDA-APHIS-PPQ, APO AA, Miami, FL.

[4] Tropical Fruit and Vegetable Research Laboratory, USDA-ARS, P.O. Box 4459, Hilo, HI 96720. Current address: Western Cotton Research Laboratory, USDA-ARS, 4135 E. Broadway Road, Phoenix, AZ 85040.

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tiated a series of observational studies in field cages to characterize male–female interactions of wild and sterile *C. capitata* and to identify where in the courtship sequence lapses in mating competitiveness of sterile males might be occurring. These tests included laboratory-reared and wild flies from Hawaiian and Central American strains. One of the Hawaiian wild strains was from the island of Kauai, where we previously documented "resistance" of the local *C. capitata* population to SIT (McInnis et al. 1996).

Materials and Methods

Sources of Insects. For production of sterile flies, *C. capitata* from the "Hi-Lab" strain were reared on artificial diet and irradiated (120 Gy minimum dose from a ^{137}Cs or ^{60}Co source; see Walker et al. [1997] for detailed information on dose range) under hypoxia at ≈48 h before adult emergence. In Hawaii, insects were reared on a wheat-based artificial diet at the USDA-ARS Tropical Fruit and Vegetable Laboratory in Honolulu or the USDA-APHIS Hawaii Fruit Fly Rearing Facility in Waimanalo (Tanaka et al. 1982). The Hi-Lab strain had been in laboratory culture for ≈500 generations during the period when the tests were run. In Guatemala, flies were reared on a sugar cane bagasse-based diet at the Moscamed-Guatemala rearing facility in Petapa. The "Petapa" strain was originally collected in southwestern Guatemala and had been in culture for ≈150 generations. Flies from genetic sexing strains came from the Vienna-42 and Tolimán-*tsl* strains. Vienna-42 is a strain of mixed Mediterranean origin and contains a temperature-sensitive lethal (*tsl*) trait that was developed and linked via a translocation to females (Franz et al. 1994). Tolimán-*tsl* contains the same *tsl* trait, but, apart from the Y chromosome, its genome is Guatemalan in origin.

Wild flies were collected as larvae in the fruit of coffee, *Coffea arabica* L., and peaches, *Prunus persica* L. Ripe coffee berries were collected from commercial plantings in Guatemala and, in Hawaii, on the islands of Kauai, Maui, and Hawaii (Kona region). Ripe peaches were collected in Kula, Maui, primarily from roadside trees and back-door plantings. Fruit was placed on paper towels and held on hardware-cloth racks above a pupation medium (vermiculite, sand, or sawdust) at room temperature (25 ± 3°C) and 75–100% RH. Pupae were gently sifted from the pupation medium every 2–4 d. For testing, the resulting insects were classified by site of origin as "Guatemala," "Maui/Kona," or "Kauai." Kauai flies came from a population that previously showed "resistance" to releases of sterile Hi-Lab flies (McInnis et al. 1996) and thus were considered separately from other Hawaiian wild flies.

Adult flies were separated by sex within 24 h of emergence. Flies were placed in screen cages and provided with food (1:3 mixture of yeast hydrolysate to sucrose; wild flies were also provided with spun honey) and water. They were held at 25 ± 2°C and 50–70% RH for 5–7 (sterile) or 9–15 (wild) d to allow for sexual maturation (flies from the laboratory colonies mature more rapidly than do wild flies).

Test Procedures. Male–female interactions were observed in walk-in outdoor screen cages at the University of Hawaii Experiment Station in Waimanalo (Oahu), HI (a total of 15 tests across seven test dates), and in a coffee plantation, Finca San Augustin, outside of Guatemala City (24 tests; nine dates). Each cage (3 m diameter, 2–2.3 m high, 18 mesh nylon) was placed over a ≈2 m tall host plant that was rooted in the earth. Coffee bushes were used in Guatemala and in two replicates in Hawaii. Guava trees, *Psidium guajava* L., were used in the remaining tests.

For testing, 25 flies of each sex from a wild strain and a laboratory strain (sterilized) were released into a cage within 2 h after sunrise. Flies from the laboratory strain were marked with a dot of white paint (AD&D Acrylic, Ral Partha Enterprises, Cincinnati, OH) on the thorax to enable the observers to distinguish them from wild flies. For the next 3–4 h (a few tests were extended to 6 h), we observed interactions that occurred when a fly approached another fly of the opposite sex. For each interaction, we recorded the following: type of male and female involved and whether the male (1) was "calling" (releasing pheromone), (2) was or began fanning his wings when the female approached, (3) began the courtship ritual (head rocking and alternating high and low amplitude wing fanning), (4) mounted the female, and (5) was successful in copulating with the female. Interactions were not included in our analyses unless they were actually observed from the initiation of the courtship sequence (approach of the female) until the interaction ended or copulation occurred. Although we attempted to observe all interactions that occurred within a cage, we believe that we typically observed only a third to a half of them. This estimate is based on comparisons of the number of successful courtships that we observed with the counts of total copulating pairs (whether or not we observed the courtship) that we made and recorded during our observations and censuses (see below). For analysis, we assumed that our observations represented an unbiased sample, i.e., we were equally likely to observe any given interaction, regardless of the types of flies involved. Tests were run with one observer per cage. All observations herein were made by one of five persons, four of whom are the authors.

During 28 of the 39 tests, cages were surveyed at half-hour intervals, and the numbers of wild and sterile males calling were counted and recorded. Because the duration of tests was variable, the number of censuses per test ranged from 5 to 12 (mean ± SD, 7.0 ± 2.0).

Contingency tables were used to determine if the proportions of counts falling into two or more distinct categories differed significantly among test groups. An example would be a test of whether the same proportions of male–female interactions culminated in copulation for wild versus sterile males. For these analyses, data were pooled across cages that contained flies from the same wild and laboratory strains. Expected values, when used, were computed for each cage and then summed across cages. Tests of significance were based on the chi-square distribution, except that the

Table 1. Observed (Obs.) and expected (Exp.) numbers of interactions between male and female *C. capitata* from various wild and sterile strains in field-cages

Source of flies			No. cages	Interactions (♂ × ♀)				χ^2	P
Wild	Sterile			S × S	W × S	S × W	W × W		
Kauai	Hi-Lab	Obs.	7	73	34	79	62	0.14	0.98
		Exp.		71.1	35.9	80.9	60.1		
Maui, Kona	Hi-Lab	Obs.	8	149	37	93	33	0.94	0.82
		Exp.		144.5	41.5	97.5	28.5		
Guatamala	Hi-Lab	Obs.	8	95	126	28	43	0.34	0.95
		Exp.		91.9	129.1	31.1	39.9		
Guatamala	Petapa	Obs.	8	54	42	37	25	0.06	0.99
		Exp.		55.4	40.6	35.6	26.4		
Guatamala	*tsl*	Obs.	8	36	18	24	36	1.18	0.76
		Exp.		31.9	22.1	28.1	31.9		

Expected numbers of each type of pairing were computed for each cage, assuming random pairing among the flies that participated in interactions in that cage. For chi-square tests, df = 3.

Fisher exact test was used for 2 × 2 tables with expected cell frequencies of <5 (Gustafson 1985).

Other analyses were conducted by computing statistics on a cage-by-cage basis, and then analyzing those statistics with paired *t*-tests or Friedman's test (SPSS 1996). Examples of these statistics include the mean number of wild versus sterile males calling (releasing pheromone) per census and the median time (H_{50}) at which flies of each strain and sex participated in mating interactions within a cage.

Results

During the 39 tests, 1,124 mating interactions were observed (30.6 ± 22.6 per test). Frequencies of interactions for each of the four possible types of pairings (e.g., sterile males with sterile females, wild males with sterile females) are shown for individual combinations of sterile and wild strains in Table 1. In no case were the observed frequencies significantly different (α = 0.05) from the frequencies that were expected, assuming random pairings of those flies that participated in interactions. Overall, participation in interactions tended to be higher among sterile flies than among wild. Interactions between sterile males and sterile females accounted for 36% of all observed interactions, whereas only 18% of interactions were between wild males and wild females. Interactions of wild males with sterile females and sterile males with wild females each accounted for 23% of the total.

Sterile males, in general, also appeared to spend more time calling than did the wild males (Table 2). The exceptions to this trend were tests in Guatemala with Hi-Lab flies (which spent ≈18 h in transport to Guatemala after irradiation) and *tsl* flies (where numbers of wild males observed calling were unusually high). For each cage, the "expected" numbers of sterile and wild males participating in interactions were computed by multiplying the total number of interactions times the proportion of total males observed calling that were, respectively, sterile or wild. The numbers of sterile males observed in mating interactions tended to be somewhat lower than the expected number, whereas wild males tended to participate in interactions to a slightly greater degree than expected (Table 2). This trend was not significant within any of the treatment groups but was consistent across all five groups.

The median time of day at which sterile and wild flies participated in male–female interactions varied among test groups. In tests in Hawaii, the median time of participation (H_{50}) was similar for sterile flies and

Table 2. Incidence of calling (releasing pheromone) and observed (Obs.) and expected (Exp.) numbers of total sexual interactions among sterile and wild male C. capitata in field cages

Strain (W/S)	No. cages	Males calling per census (±SE)	t^a	P	Total mating interactions		χ^2	P
					Obs.	Exp.		
Kauai (W)	7	1.99 ± 0.38	3.49	0.013	96	87	0.55	0.46
Hi-Lab (S)		3.55 ± 0.53			152	161		
Maui/Kona (W)	7	0.61 ± 0.24	3.67	0.010	62	50	1.35	0.25
Hi-Lab (S)		2.34 ± 0.70			219	231		
Guatemala (W)	5	2.35 ± 0.63	0.31	0.770	149	137	0.95	0.33
Hi-Lab (S)		2.09 ± 0.59			108	120		
Guatemala (W)	4	1.14 ± 0.71	3.32	0.045	49	37	2.20	0.14
Petapa (S)		1.78 ± 0.89			70	82		
Guatemala (W)	5	2.73 ± 1.18	0.56	0.604	28	19	2.41	0.12
tsl (S)		3.07 ± 0.82			26	35		

Expected numbers of males participating in mating interactions were computed for each cage based on relative proportions of wild and sterile males calling and were then summed across cages. For chi-square tests, df = 1.

[a] Paired *t*-test; df = $N - 1$.

Table 3. Median times of participation in male-female interactions (H_{50}) for laboratory-reared and wild Mediterranean fruit flies in field-cage observtaions

Source of flies		No. cages	Mean H_{50} (±SE)				χ^{2a}	P
Wild	Sterile		S ♂♂	W ♂♂	S ♀♀	W ♀♀		
Kauai	Hi-Lab	7	9:51 ± 0:17	11:01 ± 0.26	9:10 ± 0:24	10:54 ± 0:24	9.69	0.021
Maui, Kona	Hi-Lab	8	9:17 ± 0:22	9:14 ± 0:31	9:04 ± 0:26	9:20 ± 0:26	2.57	0.463
Guatamala	Hi-Lab	8	9:49 ± 0:10	9:54 ± 0:06	9:55 ± 0:07	9:32 ± 0:07	7.06	0.070
Guatamala	Petapa	8	9:55 ± 0:10	9:38 ± 0:09	10:04 ± 0:13	9:32 ± 0:12	14.59	0.002
Guatamala	*tsl*	8	10:04 ± 0:13	10:10 ± 0:11	10:10 ± 0:15	9:46 ± 0:11	3.64	0.303

[a] Chi-square approximation from Friedman's test (SPSS 1996).

wild flies from Maui and Kona. Kauai wild males and females, though, tended to participate in mating much later than did the sterile flies (Table 3). In contrast, Guatemalan wild flies (especially females) tended, if anything, to participate in interactions earlier than the sterile flies did. With Petapa sterile flies, this produced significant variation in H_{50}.

Of the 1,124 total interactions, 242 (21.5%) culminated in copulation. Percentages of interactions that ended with copulation varied widely (1.3–48%) depending on the types of males and females involved. The most prominent trend in the data was that wild females accepted wild males more readily than they accepted sterile males. This trend was (numerically) consistent across all five series of tests and was significant in three of the five (Fig. 1). Also, wild females from Hawaii (and especially Kauai) tended to accept males of either type less readily than did wild females in the Guatemala tests. Trends of mate acceptance were less consistent among sterile females. Perhaps surprisingly, sterile Hi-Lab females tended to accept wild males from Hawaii more readily (and, with Kauai males, significantly more readily) than they accepted males from their own strain (Fig. 1). In Guatemala, though, Hi-Lab females appeared to prefer Hi-Lab males to wild males, although this effect was not significant ($P = 0.051$). Females from the Petapa and *tsl* strains did not show measurable preferences for wild versus sterile males (Fig. 1).

Males from all strains initiated courtship on the vast majority (96% overall) of occasions when a female approached them. Most of these courtship sequences (653 of 1075; 61%) went to completion; that is, they culminated in the male mounting the female. The other 39% of courtships ended either when the male or (more often) the female walked or flew away or when the courtship was disrupted by a third fly. When the male mounted the female, the female usually dropped off of the substrate (typically, the bottom of a leaf) and shook the male off (411 of 653; 63%). In the other 242 occasions, copulation occurred.

Wild females displayed reduced acceptance of sterile males both before and after mounting. For all five of the test groupings, the proportion of courtships that culminated in males mounting wild females was numerically lower for sterile males than for wild males; for three of the five groups the difference was significant (Fig. 2). Similarly, the proportions of mounted couples that actually copulated were always numerically lower for sterile male-wild female couples than for wild-wild couples, although these differences were significant in only one instance (Fig. 3). Depending on the strains involved, the relative preference of wild females for wild males manifested itself primarily before mounting occurred (Petapa males), after mounting (*tsl* males), or at both times (Hawaiian wild females). For Hi-Lab females, differential responses to sterile versus wild males manifested themselves primarily after mounting occurred (Figs. 2 and 3).

Discussion

Sterile male *C. capitata* have typically appeared less than fully competitive with wild males when released

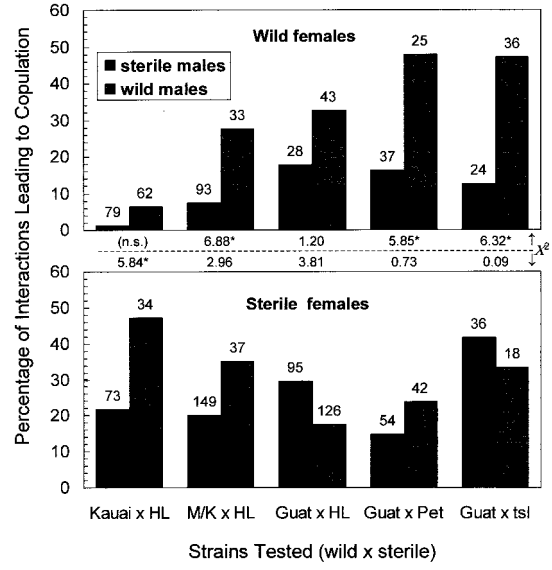

Fig. 1. Percentages of mating interactions that culminated in copulation in field cages containing wild and sterile *C. capitata.* Wild strains were from coffee berries collected in Hawaii on the islands of Maui and Hawaii (M/K) or Kauai, or in Guatemala (Guat); sterile flies were reared in Hawaii (HL) or Guatemala (Pet, tsl). Numbers above bars represent total interactions observed; numbers between graphs are values of chi-square for proportions of wild (top line) or sterile females that mated with sterile versus wild males (* indicates that the chi-square is significant at $\alpha = 0.05$; n.s. = not significantly different, as determined by Fisher exact test).

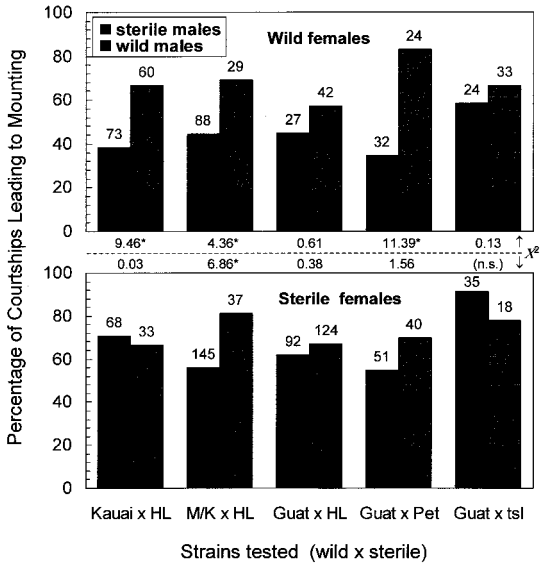

Fig. 2. Percentages of courtship displays that culminated in the male mounting the female in field cages containing wild and sterile *C. capitata.* Wild strains were from coffee berries collected in Hawaii on the islands of Maui and Hawaii (M/K) or Kauai, or in Guatemala (Guat); sterile flies were reared in Hawaii (HL) or Guatemala (Pet, tsl). Numbers above bars represent total courtships observed; numbers between graphs are values of chi-square for proportions of wild (top line) or sterile females that mated with sterile versus wild males (* indicates that the chi-square is significant at $\alpha = 0.05$; n.s. = not significantly different, as determined by Fisher exact test).

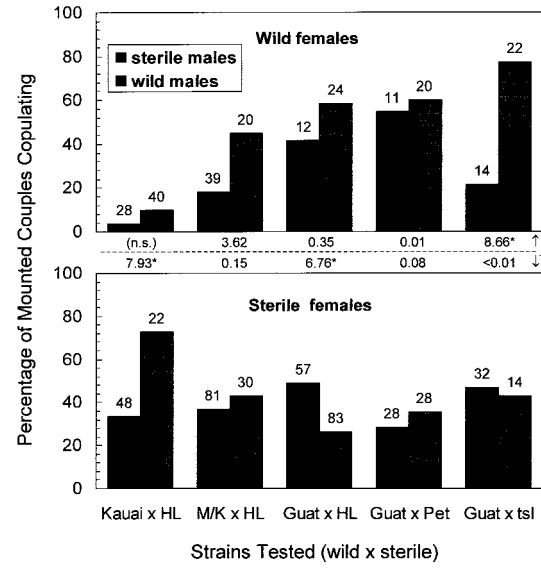

Fig. 3. Percentages of mounted couples that proceeded to copulate in field cages containing wild and sterile *C. capitata.* Wild strains were from coffee berries that were collected in Hawaii on the islands of Maui and Hawaii (M/K) or Kauai, or in Guatemala (Guat); sterile flies were reared in Hawaii (HL) or Guatemala (Pet, tsl). Numbers above bars represent total mounted couples observed; numbers between graphs are values of chi-square for proportions of wild (top line) or sterile females that mated with sterile versus wild males (* indicates that the chi-square is significant at $\alpha = 0.05$; n.s. = not significantly different, as determined by Fisher exact test).

into the field (Wong et al. 1992, McInnis et al. 1994, Shelly et al. 1994, Shelly and Whittier 1996). After observing sterile males actively calling and participating in mating aggregations, Shelly et al. (1994) suggested that the sterile males' poor competitiveness was likely caused, at least in part, by their reduced ability to perform courtship acceptable to the wild females. Results of our observations support this contention.

In the field cages, numbers of sterile males that we observed calling were similar to, or greater than, the numbers of wild males calling. Among calling males, the ability of sterile males to attract females into their vicinity appeared comparable to (or nearly so) that of wild males (also see Heath et al. [1994] and references therein). In addition, the apparent random distribution of interactions we observed among wild and sterile flies suggests that both wild and sterile males were capable of attracting wild and sterile females into their vicinity. Thus, the assortative mating that has been observed in other studies with sterile and wild flies (e.g., Shelly et al. 1994, McInnis et al. 1996, Shelly and Whittier 1996) most likely resulted from the ways in which females from different strains responded to the courtships of wild versus sterile males.

The one precourtship factor that varied significantly among strains and sexes was the time of day at which flies participated in male–female interactions. In Guatemala, mating activities of wild females tended to be earlier than that of sterile flies. In Hawaii, though, mating activity of wild flies of both sexes from Kauai was substantially delayed. Behavioral resistance of wild flies to releases of Hi-Lab sterile flies apparently developed during an extended pilot-scale SIT program on Kauai (McInnis et al. 1996). Although it is tempting to point to differences in sexual periodicity as a possible mechanism of mating isolation between wild and sterile flies, the delayed sexual activity of Kauai wild flies did not appear to result in an excess of wild:wild or sterile:sterile interactions in our tests (see Table 1). In field-cage tests in which copulating pairs were collected in vials, we likewise found that wild flies from Kauai (but not from other Hawaiian islands) tended to mate later than did sterile flies (D.O.M., D.R.L., and C.G.J., unpublished data). This difference in sexual periodicity, though, accounted for only a small portion of the mating isolation that we observed.

Clearly, the wild females in our tests tended to accept the courtship overtures of wild males more readily than they accepted those of sterile males. Courtship in *C. capitata* likely involves visual, auditory, chemical, and perhaps mechanical cues, and wild females presumably discriminate between wild and sterile males on the basis of differences in one or more of these sensory modalities. During our observations, the courtship behavior of wild and sterile males appeared qualitatively similar. Both types of males exhibited all

of the typical behaviors that are known to be part of the courtship and performed them in (apparently) the proper order (see Feron 1962, Briceño et al. 1996, Liimatainen et al. 1997). Females, then, are likely detecting quantitative differences in courtship behavior, and, indeed, analyses of videotaped courtships have detected differences between sterile and wild males in the frequency and duration of certain components of the courtship sequence (Briceño and Eberhard 1998; D.R.L., unpublished data). Similarly, Heath et al. (1994) found quantitative differences in the release of four major pheromone components of *C. capitata* among wild, laboratory-produced, and irradiated males. The pheromone produced by the sterile males could possibly be adequate for attracting wild females into their vicinity, but less than optimal during courtship.

Whatever their cause, low acceptance rates of sterile males by wild females will reduce the efficiency and cost-effectiveness of SIT programs (Barclay 1982, Calkins and Ashley 1989, but see Tsubaki and Bunroongsook 1990). Current procedures for colonization and maintenance of *C. capitata* cultures tend to reduce the genetic, physiological, and, apparently, behavioral competence of a strain (Leppla et al. 1983, Saul and McCombs 1995). Our results indicate that these changes will tend to reduce the acceptability of laboratory-reared male *C. capitata* to wild females in target populations. Although this reduction in acceptability is normally not severe enough to preclude the effective use of SIT (Cayol et al. 1999), it reduces the efficiency and cost-effectiveness of SIT programs and increases the likelihood that resistance can develop (Calkins and Ashley 1989, McInnis et al. 1996). Improved methods for developing and maintaining new strains are needed to ensure high levels of mating compatibility between wild and sterile flies.

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